

On global stability of the Lotka reactions with generalized mass-action kinetics

Balázs Boros · Josef Hofbauer ·
Stefan Müller

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Abstract Chemical reaction networks with generalized mass-action kinetics lead to power-law dynamical systems. As a simple example, we consider the Lotka reactions with two chemical species and arbitrary power-law kinetics. We study existence, uniqueness, and stability of the positive equilibrium, in particular, we characterize its global asymptotic stability in terms of the kinetic orders.

Keywords chemical reaction network · power-law kinetics · Andronov-Hopf bifurcation · Dulac function

1 Introduction

Lotka [10] considered a series of chemical reactions, $S \rightarrow X$, $X \rightarrow Y$, and $Y \rightarrow P$, which transform a substrate into a product. If the first and the second reaction are assumed to be autocatalytic in X and Y , respectively, then the resulting dynamics is equivalent to the classical Lotka-Volterra predator-prey system [11, 12].

Farkas and Noszticzius [4] and Dancsó et al. [3] considered generalized Lotka-Volterra schemes, that is, the Lotka reactions with power-law kinetics (and non-negative real exponents), and provided a local stability analysis as well as first integrals. We continue this line of research and consider the Lotka reactions with *arbitrary* power-law kinetics. Moreover, we provide a *global* stability analysis.

As in the example of the Lotka reactions, every chemical reaction network with generalized mass-action kinetics (power-law kinetics) leads to a generalized mass-action system. For such systems, Müller and Regensburger [13, 14] analyzed existence and uniqueness of (special) equilibria. The works [4, 3] and the present work are first steps towards an understanding of their stability.

Balázs Boros and Stefan Müller
Radon Institute for Computational and Applied Mathematics,
Austrian Academy of Sciences, Altenbergerstrasse 69, 4040 Linz, Austria
E-mail: balazs.boros@ricam.oeaw.ac.at, stefan.mueller@ricam.oeaw.ac.at

Josef Hofbauer
Faculty of Mathematics, University of Vienna,
Oskar-Morgenstern-Platz 1, 1090 Vienna, Austria
E-mail: josef.hofbauer@univie.ac.at

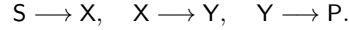
In a classical Lotka-Volterra system, the unique positive equilibrium is neutrally stable, and all other positive solutions are periodic, corresponding to closed orbits. Generically, a Lotka-Volterra scheme still has a unique positive equilibrium, but it can be stable or unstable. The corresponding Andronov-Hopf bifurcation can be supercritical, subcritical, or degenerate leading to asymptotically stable, repelling, or a continuum of closed orbits.

As our main result, we characterize global asymptotic stability of the unique positive equilibrium in terms of the kinetic orders. Thereby, we apply the Bendixson-Dulac test in order to rule out periodic solutions. Further, we rule out unbounded solutions and solutions approaching the boundary of the positive quadrant.

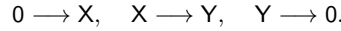
The paper is organized as follows. In Section 2, we motivate generalized Lotka-Volterra schemes as chemical reaction networks with generalized mass-action kinetics. In Section 3, we present our main results, and in Section 4, we provide the corresponding proofs.

2 Lotka-Volterra schemes as generalized mass-action systems

As in the original work by Lotka [10], we start by considering a series of irreversible chemical reactions,



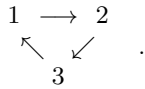
The first reaction turns a substrate into species X , the second reaction transforms X into Y , and the third reaction turns species Y into a product or degrades it. We are interested in the dynamics of X and Y only, in particular, we assume that the substrate is present in constant amount and that the product does not affect the dynamics. As a consequence, we can omit substrate and product from consideration, and obtain the simplified reactions



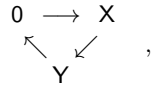
To obtain a classical Lotka-Volterra system as in [11,12], we assume the first and the second reaction to be autocatalytic, in particular, we define the kinetics of the reactions as

$$v_{0 \rightarrow X} = k_{0 \rightarrow X}[X], \quad v_{X \rightarrow Y} = k_{X \rightarrow Y}[X][Y], \quad v_{Y \rightarrow 0} = k_{Y \rightarrow 0}[Y]$$

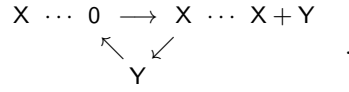
with rate constants $k_{0 \rightarrow X}, k_{X \rightarrow Y}, k_{Y \rightarrow 0} > 0$. In terms of chemical reaction network theory (CRNT), we specify the system as a chemical reaction network with generalized mass-action kinetics, that is, as a generalized mass-action system [13,14]. The network arises from a directed graph with edges representing reactions,



To each node, we assign a (stoichiometric) complex to determine the stoichiometry of the network,



and additionally a kinetic-order complex to determine the kinetics,



For the third node, we do not state the kinetic-order complex explicitly since it coincides with the stoichiometric complex. The resulting ODE for the concentrations $x = [X]$ and $y = [Y]$ is given by

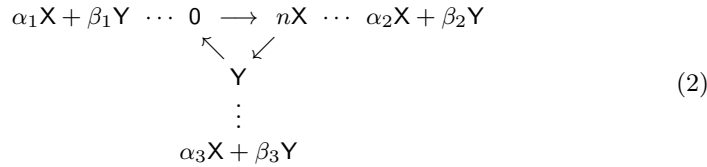
$$\begin{aligned} \dot{x} &= k_{12} x - k_{23} xy, \\ \dot{y} &= k_{23} xy - k_{31} y \end{aligned} \quad (1)$$

with $k_{12} = k_{0 \rightarrow X}$, $k_{23} = k_{X \rightarrow Y}$, $k_{31} = k_{Y \rightarrow 0}$.

In this work, we consider more general stoichiometry and kinetics. In the second reaction, we allow that X and Y have different stoichiometric coefficients, in particular, we consider $nX \longrightarrow Y$ with $n > 0$. Further, we allow general power-law kinetics for all reactions,

$$v_{12} = k_{12}[X]^{\alpha_1}[Y]^{\beta_1}, \quad v_{23} = k_{23}[X]^{\alpha_2}[Y]^{\beta_2}, \quad v_{31} = k_{31}[X]^{\alpha_3}[Y]^{\beta_3}$$

with exponents $\alpha_1, \beta_1, \alpha_2, \beta_2, \alpha_3, \beta_3 \in \mathbb{R}$. Also this system can be specified as a chemical reaction network with generalized mass-action kinetics, that is, as a directed graph with stoichiometric and kinetic-order complexes:



The resulting ODE is given by

$$\begin{aligned} \dot{x} &= nk_{12} x^{\alpha_1} y^{\beta_1} - nk_{23} x^{\alpha_2} y^{\beta_2}, \\ \dot{y} &= k_{23} x^{\alpha_2} y^{\beta_2} - k_{31} x^{\alpha_3} y^{\beta_3}. \end{aligned}$$

In order to define the dynamics on the *non-negative* quadrant, one allows only non-negative exponents. Further, in order to ensure forward-invariance of the non-negative quadrant, one requires $\alpha_2, \beta_3 > 0$. However, in this work, we allow real exponents and consider the dynamics on the *positive* quadrant.

In CRNT, one is often interested in results for *all* rate constants (and given stoichiometry), in our example, in existence, uniqueness, and stability of equilibria for all k_{12}, k_{23}, k_{31} (and given n).

Finally, we introduce the parameters

$$k_1 = nk_{12}, \quad k_2 = nk_{23}, \quad k_3 = k_{23}, \quad k_4 = k_{31}, \quad (3)$$

which are in one-to-one correspondence with the stoichiometric coefficient n and the rate constants k_{12}, k_{23}, k_{31} , and obtain a generalized Lotka-Volterra scheme [4, 3],

$$\begin{aligned} \dot{x} &= k_1 x^{\alpha_1} y^{\beta_1} - k_2 x^{\alpha_2} y^{\beta_2}, \\ \dot{y} &= k_3 x^{\alpha_2} y^{\beta_2} - k_4 x^{\alpha_3} y^{\beta_3}. \end{aligned} \quad (4)$$

For the technical analysis, we often consider an ODE which is orbitally equivalent on the positive quadrant and has two exponents less,

$$\begin{aligned}\dot{x} &= k_1 x^{a_1} y^{b_1} - k_2, \\ \dot{y} &= k_3 - k_4 x^{a_3} y^{b_3},\end{aligned}\tag{5}$$

where $a_1 = \alpha_1 - \alpha_2$, $b_1 = \beta_1 - \beta_2$, $a_3 = \alpha_3 - \alpha_2$, $b_3 = \beta_3 - \beta_2$. Dancsó et al. [3] studied the ODE (4) in another orbitally equivalent form,

$$\begin{aligned}\dot{x} &= k_1 x^{\hat{p}} - k_2 x^p y^q, \\ \dot{y} &= k_3 x^p y^q - k_4 y^{\hat{q}},\end{aligned}\tag{6}$$

where $\hat{p} = \alpha_1 - \alpha_3$, $\hat{q} = \beta_3 - \beta_1$, $p = \alpha_2 - \alpha_3$, $q = \beta_2 - \beta_1$. The authors carried out a stability analysis, in particular, they studied the Andronov-Hopf bifurcation of the unique positive equilibrium (provided it exists) and a so-called zip bifurcation. In this work, we provide a global stability analysis.

3 Main results

We investigate the ODE (4), in particular, we are interested in the qualitative dynamics on the positive quadrant \mathbb{R}_+^2 . We call a positive equilibrium *globally asymptotically stable* if it is Lyapunov stable and from each positive initial conditions the solution converges to the equilibrium.

We introduce

$$C = \begin{pmatrix} a_1 & b_1 \\ a_3 & b_3 \end{pmatrix} = \begin{pmatrix} \alpha_1 - \alpha_2 & \beta_1 - \beta_2 \\ \alpha_3 - \alpha_2 & \beta_3 - \beta_2 \end{pmatrix} \quad \text{and} \quad k = (k_1, k_2, k_3, k_4) \in \mathbb{R}_+^4 \tag{7}$$

and start by examining the number of equilibria.

Proposition 1 *For the ODE (4), the following statements hold.*

- (i) *If $\det C \neq 0$, then there exists a unique positive equilibrium (x^*, y^*) given by*

$$x^* = \left(\frac{k_2}{k_1}\right)^{\frac{b_3}{\det C}} \left(\frac{k_3}{k_4}\right)^{-\frac{b_1}{\det C}} \quad \text{and} \quad y^* = \left(\frac{k_2}{k_1}\right)^{-\frac{a_3}{\det C}} \left(\frac{k_3}{k_4}\right)^{\frac{a_1}{\det C}}. \tag{8}$$

- (ii) *If $\det C = 0$, then the set of positive equilibria is either empty or infinite, depending on k .*

We consider only the generic case (i) and assume $\det C \neq 0$ in the following. Case (ii), in particular the related zip bifurcation, was studied in detail in [3]. We proceed by examining the asymptotic stability of the unique positive equilibrium using linearization.

Proposition 2 *Assume $\det C \neq 0$ and let (x^*, y^*) be the unique positive equilibrium of the ODE (4). Then the following statements hold.*

(i) The Jacobian matrix J at (x^*, y^*) is given by

$$\begin{aligned} J &= (x^*)^{\alpha_2} (y^*)^{\beta_2} \begin{pmatrix} k_2 & 0 \\ 0 & k_3 \end{pmatrix} \begin{pmatrix} a_1 & b_1 \\ -a_3 & -b_3 \end{pmatrix} \begin{pmatrix} \frac{1}{x^*} & 0 \\ 0 & \frac{1}{y^*} \end{pmatrix} \\ &= (x^*)^{\alpha_2} (y^*)^{\beta_2} \begin{pmatrix} a_1 \frac{k_2}{x^*} & b_1 \frac{k_2}{y^*} \\ -a_3 \frac{k_3}{x^*} & -b_3 \frac{k_3}{y^*} \end{pmatrix} \end{aligned}$$

and hence

$$\begin{aligned} \text{sign}(\det J) &= -\text{sign}(\det C), \\ \text{sign}(\text{tr } J) &= \text{sign} \left(a_1 \frac{k_2}{x^*} - b_3 \frac{k_3}{y^*} \right). \end{aligned}$$

(ii) The linearization at (x^*, y^*) is asymptotically stable if and only if $\det C < 0$ and $a_1 \frac{k_2}{x^*} - b_3 \frac{k_3}{y^*} < 0$.

We are also interested in asymptotic stability when the trace of the Jacobian matrix vanishes, that is, when linearization does not give any information.

Proposition 3 For the ODE (4), assume $\det C < 0$ and $a_1 \frac{k_2}{x^*} - b_3 \frac{k_3}{y^*} = 0$. Further, let

$$d_1 = a_3[(1 + a_3 - a_1)b_1b_3 - a_1a_3(1 + b_1 - b_3)].$$

Then the following statements hold.

- (i) If $d_1 < 0$, the unique positive equilibrium is asymptotically stable. If $d_1 > 0$, it is repelling.
- (ii) If we consider a one-parameter family of ODEs (4) along which the eigenvalues of the Jacobian matrix cross the imaginary axis with positive speed, for example, with parameter $\mu = a_1 \frac{k_2}{x^*} - b_3 \frac{k_3}{y^*}$, then an Andronov-Hopf bifurcation occurs at $\mu = 0$. If $d_1 < 0$, the bifurcation is supercritical (and there exists an asymptotically stable closed orbit for small $\mu > 0$). If $d_1 > 0$, it is subcritical (and there exists a repelling closed orbit for small $\mu < 0$).

This result is essentially Theorem 1 in Dancsó et al. [3], apart from the expression d_1 for the first focal value. For details, see Subsection 4.2.2.

If $a_1 = b_3 = 0$ (and hence $d_1 = 0$) and $a_3b_1 > 0$, then the unique positive equilibrium is a center, which can be shown by finding a first integral, see [4]. This includes the classical Lotka-Volterra system (1), where $a_3 = b_1 = -1$. For further details, see Subsection 4.2.3.

Remark. Llibre [9] claims that Theorem 1 in Dancsó et al. [3] is wrong and provides the following “counter example”: $\alpha_1 = \beta_3 = 1$, $\beta_1 = \alpha_3 = 0$, $\alpha_2 = \beta_2 = 2$, $k_1 = k_2 = 1$, $k_3 = k_4 = 1 + \mu$ and hence $a_1 = b_3 = -1$, $b_1 = a_3 = -2$, $x^* = y^* = 1$, $\det C < 0$, and $a_1 \frac{k_2}{x^*} - b_3 \frac{k_3}{y^*} = \mu$. As a result, one has $d_1 = 0$ (also from the incorrect expression in Theorem 1 in [3]), and the nature of the Andronov-Hopf bifurcation is not determined by the first focal value. For $\mu = 0$, there is a first integral $H(x, y) = x + y + \frac{1}{xy}$, see [9] or already [3] (p. 122, Table I, case (ii) with $\hat{p} = \hat{q} = 1$, $p = q = 2$). Therefore the Andronov-Hopf bifurcation is degenerate, that is, all closed orbits occur at $\mu = 0$. Llibre’s “counter example” is an explicit example of a degenerate Andronov-Hopf bifurcation which was already well described by Dancsó

et al. Without explaining it, Llibre uses a terminology which is non-standard in the dynamical systems community. The case of a degenerate Andronov-Hopf bifurcation (where all periodic solutions appear at the critical parameter value) is included in most treatments of this theory, starting with the original theorems of Andronov and Leontovich [1] and Hopf [8]. See, for example, Lemma 7.2.5 and Theorem 7.2.3 in [5].

Next, we characterize the exponents $\alpha_1, \beta_1, \alpha_2, \beta_2, \alpha_3, \beta_3$ in the ODE (4) for which the unique positive equilibrium is asymptotically stable for all parameters k . Recall that k depends on the rate constants k_{12}, k_{23}, k_{31} and the stoichiometric coefficient n of the underlying chemical reaction network (2). As usual in CRNT, we are also interested in statements which hold for all rate constants, but given stoichiometry, that is, for all k with $k_2 = nk_3$, see Equations (3).

Theorem 4 *Assume $\det C \neq 0$, that is, for all parameters k , the ODE (4) admits a unique positive equilibrium. Further, let $n > 0$. Then the following statements are equivalent.*

- (i) *For all k , the unique positive equilibrium is asymptotically stable.*
- (ii) *For all k with $k_2 = nk_3$, the unique positive equilibrium is asymptotically stable.*
- (iii) *$\det C < 0$, $a_1 \leq 0 \leq b_3$, and $(a_1, b_3) \neq (0, 0)$.*

After ruling out periodic solutions, unbounded solutions, and solutions approaching the boundary of the positive quadrant, we find that – apart from some boundary cases – global asymptotic stability for all k follows from asymptotic stability for all k .

Theorem 5 *Assume $\det C \neq 0$, that is, for all parameters k , the ODE (4) admits a unique positive equilibrium. Further, let $n > 0$. Then the following statements are equivalent.*

- (i) *For all k , the unique positive equilibrium is globally asymptotically stable.*
- (ii) *For all k with $k_2 = nk_3$, the unique positive equilibrium is globally asymptotically stable.*
- (iii) *$\det C < 0$ and either*
 - *$a_1 < 0 < b_3$,*
 - *$a_1 < 0 = b_3$, $a_3 < 0$, and $b_1 \leq -1$, or*
 - *$a_1 = 0 < b_3$, $a_3 \leq -1$, and $b_1 < 0$.*

In preparation of our final result, we provide sufficient conditions for precluding global asymptotic stability.

Proposition 6 *For the ODE (4), assume $\det C < 0$ and one of the following four conditions.*

- *$a_1 < 0$, $b_1 < 0$, $a_3 < 0$, $b_3 < 0$, and $(0 < 1 + b_1 - b_3$ or $\det C > a_3 + b_3)$.*
- *$a_1 < 0$, $b_1 > 0$, $a_3 > 0$, $b_3 < 0$, and $\det C > a_3 + b_3$.*
- *$a_1 > 0$, $b_1 > 0$, $a_3 > 0$, $b_3 > 0$.*
- *$a_1 > 0$, $b_1 < 0$, $a_3 < 0$, $b_3 > 0$, and $(a_1 > 1$ or $a_1 + b_1 > 0)$.*

Then there exists a solution which does not converge to the unique positive equilibrium.

Finally, we characterize (global) asymptotic stability of the unique positive equilibrium for given k . To reduce the complexity of the problem, we analyze the special case $\alpha_1 = \alpha$, $\beta_1 = 0$, $\alpha_2 = 1$, $\beta_2 = \beta$, $\alpha_3 = 0$, $\beta_3 = 1$ with $\alpha, \beta \in \mathbb{R}$. That is, we consider the ODE

$$\begin{aligned}\dot{x} &= k_1 x^\alpha - k_2 xy^\beta, \\ \dot{y} &= k_3 xy^\beta - k_4 y.\end{aligned}\tag{9}$$

In terms of the underlying chemical reaction network (2), we study two consecutive autocatalytic reactions with kinetic orders α and β , respectively, and a degradation reaction. To ease the notation, we further assume $k_1 = k_2 = k_3 = k_4 = 1$.

Theorem 7 *For the ODE (9), assume $\alpha\beta - \alpha + 1 \neq 0$ and $k_1 = k_2 = k_3 = k_4 = 1$. Then the following statements hold.*

- (i) *There exists a unique positive equilibrium, namely $(1, 1)$, and the Jacobian matrix J at $(1, 1)$ is given by*

$$J = \begin{pmatrix} \alpha - 1 & -\beta \\ 1 & \beta - 1 \end{pmatrix}.$$

- (ii) *The equilibrium $(1, 1)$ is asymptotically stable if and only if*

$$\alpha\beta - \alpha + 1 > 0, \alpha + \beta \leq 2, \text{ and } (\alpha, \beta) \neq (1, 1).$$

- (iii) *If $\alpha\beta - \alpha + 1 > 0$, $\alpha + \beta = 2$, and $(\alpha, \beta) \neq (1, 1)$, then the equilibrium $(1, 1)$ is asymptotically stable and undergoes a supercritical Andronov-Hopf bifurcation.*
 (iv) *If $(\alpha, \beta) = (1, 1)$, then the equilibrium $(1, 1)$ is a center, and all solutions in the positive quadrant are periodic.*
 (v) *The equilibrium $(1, 1)$ is globally asymptotically stable if and only if $\alpha\beta - \alpha + 1 > 0$ and either*
- $\alpha \leq 1$, $\beta \leq 1$, and $(\alpha, \beta) \neq (1, 1)$, or
 - $1 < \alpha \leq \frac{3}{2}$ and $\alpha - 1 \leq \beta \leq 2 - \alpha$.

Figure 1 illustrates our main results, in particular, the stability properties of the unique positive equilibrium of the ODE (9). We depict regions in the (α, β) -plane which result in stable or unstable behavior either for all parameters k or for $k_1 = k_2 = k_3 = k_4 = 1$.

4 Proofs

It remains to prove the results presented in Section 3.

4.1 Number of equilibria: Proposition 1

Using the notation (7), a positive equilibrium $(x, y) \in \mathbb{R}_+^2$ of the ODE (4) is determined by

$$x^{a_1} y^{b_1} = \frac{k_2}{k_1} \quad \text{and} \quad x^{a_3} y^{b_3} = \frac{k_3}{k_4}$$

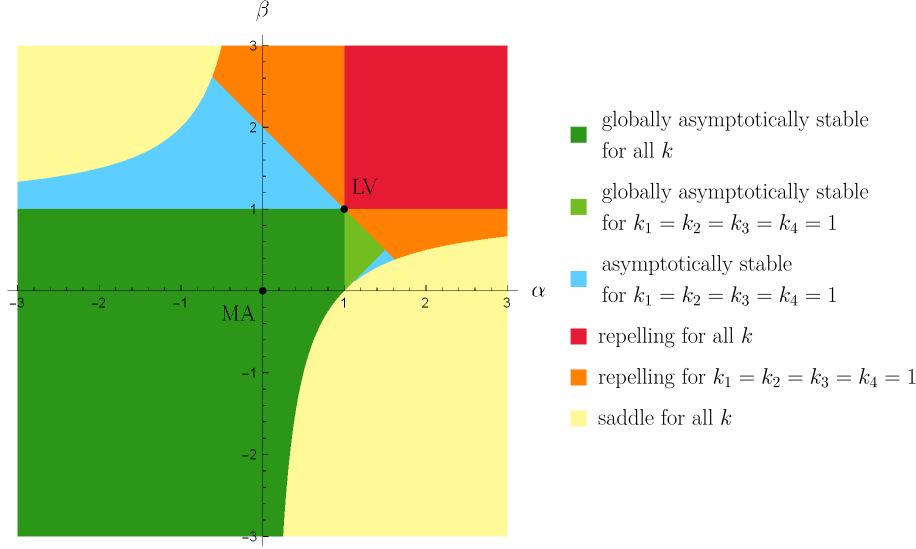


Figure 1 Stability of the unique positive equilibrium of the ODE (9) depending on the exponents (α, β) . The special case $(\alpha, \beta) = (1, 1)$ is a classical Lotka-Volterra system, while $(\alpha, \beta) = (0, 0)$ is a linear mass-action system.

or, equivalently, by

$$\begin{pmatrix} a_1 & b_1 \\ a_3 & b_3 \end{pmatrix} \begin{pmatrix} \ln x \\ \ln y \end{pmatrix} = \begin{pmatrix} \ln \frac{k_2}{k_1} \\ \ln \frac{k_3}{k_4} \end{pmatrix}.$$

If $\det C \neq 0$, there exists a unique positive equilibrium, and a short calculation shows that it is given by Equations (8). If $\det C = 0$, the set of equilibria is either infinite or empty depending on whether the vector $(\ln \frac{k_2}{k_1}, \ln \frac{k_3}{k_4})^T$ is in the image of C or not. This concludes the proof of Proposition 1.

4.2 Asymptotic stability of the unique positive equilibrium

We prove Proposition 2, compute the first focal value stated in Proposition 3, discuss the special case $(a_1, b_3) = (0, 0)$, and prove Theorem 4. See the corresponding Subsections 4.2.1, 4.2.2, 4.2.3, and 4.2.4.

4.2.1 The Jacobian matrix at the unique positive equilibrium: Proposition 2

Assume $\det C \neq 0$ for the ODE (4). The Jacobian matrix J at the unique positive equilibrium (x^*, y^*) is given by

$$\begin{aligned} J_{11} &= k_1 \alpha_1 (x^*)^{\alpha_1 - 1} (y^*)^{\beta_1} - k_2 \alpha_2 (x^*)^{\alpha_2 - 1} (y^*)^{\beta_2}, \\ J_{12} &= k_1 \beta_1 (x^*)^{\alpha_1} (y^*)^{\beta_1 - 1} - k_2 \beta_2 (x^*)^{\alpha_2} (y^*)^{\beta_2 - 1}, \\ J_{21} &= k_3 \alpha_2 (x^*)^{\alpha_2 - 1} (y^*)^{\beta_2} - k_4 \alpha_3 (x^*)^{\alpha_3 - 1} (y^*)^{\beta_3}, \\ J_{22} &= k_3 \beta_2 (x^*)^{\alpha_2} (y^*)^{\beta_2 - 1} - k_4 \beta_3 (x^*)^{\alpha_3} (y^*)^{\beta_3 - 1}. \end{aligned}$$

Using the equilibrium equations $k_1(x^*)^{a_1}(y^*)^{b_1} = k_2$ and $k_3 = k_4(x^*)^{a_3}(y^*)^{b_3}$, we obtain

$$J = (x^*)^{\alpha_2}(y^*)^{\beta_2} \begin{pmatrix} a_1 \frac{k_2}{x^*} & b_1 \frac{k_2}{y^*} \\ -a_3 \frac{k_3}{x^*} & -b_3 \frac{k_3}{y^*} \end{pmatrix}.$$

The factorization

$$J = (x^*)^{\alpha_2}(y^*)^{\beta_2} \begin{pmatrix} k_2 & 0 \\ 0 & k_3 \end{pmatrix} \begin{pmatrix} a_1 & b_1 \\ -a_3 & -b_3 \end{pmatrix} \begin{pmatrix} \frac{1}{x^*} & 0 \\ 0 & \frac{1}{y^*} \end{pmatrix}$$

follows directly. This concludes the proof of Proposition 2 (i) which immediately implies Proposition 2 (ii).

4.2.2 First focal value: Proposition 3

We assume $\det C \neq 0$ and use the unique positive equilibrium (x^*, y^*) to scale the ODE (5). We introduce $K = \frac{k_3}{k_2} \frac{x^*}{y^*}$ and obtain the equivalent ODE

$$\begin{aligned} \dot{x} &= f(x, y) = x^{a_1} y^{b_1} - 1, \\ \dot{y} &= g(x, y) = K \left(1 - x^{a_3} y^{b_3} \right), \end{aligned}$$

which has the unique positive equilibrium $(1, 1)$. If the equilibrium undergoes an Andronov-Hopf bifurcation, then the determinant of the Jacobian matrix is positive (that is, $\det C < 0$) and its trace is zero (that is, $a_1 = K b_3$). In order to determine the sign of the first focal value D_1 , we use Equation (19) from Appendix A. In particular, we compute the partial derivatives of f and g up to order three at $(1, 1)$. The resulting first focal value D_1 has the same sign as the expression

$$d_1 = a_3[(1 + a_3 - a_1)b_1 b_3 - a_1 a_3(1 + b_1 - b_3)].$$

In [3], the authors study the ODE (4) in the form (6). In particular, they compute the first focal value. However, Equation (22) in [3] is not correct. In their notation, the correct formula is given by

$$G = p[p(\hat{p} - p)(\hat{q} - 1) - q(\hat{q} - q)(\hat{p} - 1)].$$

We also correct the three lemmas in the Appendix of [3].

Lemma 8 (Lemma 1 in [3]) *Consider the system*

$$\dot{z}_1 = A(z_1^{a_1} - z_2^{a_2}), \quad \dot{z}_2 = B(z_1^{b_1} - z_2^{b_2}),$$

where $\det J = AB(-a_1 b_2 + b_1 a_2) > 0$ and $\text{tr } J = Aa_1 - Bb_2 = 0$. At the equilibrium $(1, 1)$, the first focal value has the same sign as

$$g = Ab_1[(1 + b_1 - a_1)a_2 b_2 - a_1 b_1(1 + a_2 - b_2)].$$

Lemma 9 (Lemma 2 in [3]) *Consider the system*

$$\dot{z}_1 = A(e^{a_1 z_1} - z_2^{a_2}), \quad \dot{z}_2 = B(e^{b_1 z_1} - z_2^{b_2}),$$

where $\det J = AB(-a_1 b_2 + b_1 a_2) > 0$ and $\operatorname{tr} J = Aa_1 - Bb_2 = 0$. At the equilibrium $(0, 1)$, the first focal value has the same sign as

$$g = -Aa_1(1 + a_2 - b_2).$$

Lemma 10 (Lemma 3 in [3]) *Consider the system*

$$\dot{z}_1 = A(e^{a_1 z_1} - e^{a_2 z_2}), \quad \dot{z}_2 = B(e^{b_1 z_1} - e^{b_2 z_2}),$$

where $\det J = AB(-a_1 b_2 + b_1 a_2) > 0$ and $\operatorname{tr} J = Aa_1 - Bb_2 = 0$. At the equilibrium $(0, 0)$, the first focal value is zero.

We note that an expression for the first focal value has been derived for planar S-systems, see [15].

4.2.3 The special case $(a_1, b_3) = (0, 0)$

We describe the behavior of the ODE (4) for $(a_1, b_3) = (0, 0)$. In particular, we find a first integral, see also [4].

In the special case $(a_1, b_3) = (0, 0)$, the ODE (4) takes the form

$$\begin{aligned} \dot{x} &= x^{\alpha_2} y^{\beta_2} (k_1 y^{b_1} - k_2), \\ \dot{y} &= x^{\alpha_2} y^{\beta_2} (k_3 - k_4 x^{a_3}). \end{aligned} \tag{10}$$

If $a_3 b_1 < 0$, then $\det C > 0$ and the unique positive equilibrium is a saddle. If $a_3 b_1 > 0$, we show that the unique positive equilibrium (x^*, y^*) is a center. Let $V: \mathbb{R}_+^2 \rightarrow \mathbb{R}$ be a continuously differentiable function with

$$\begin{aligned} (\partial_1 V)(x, y) &= k_3 \left(1 - \left(\frac{x}{x^*} \right)^{a_3} \right), \\ (\partial_2 V)(x, y) &= k_2 \left(1 - \left(\frac{y}{y^*} \right)^{b_1} \right). \end{aligned} \tag{11}$$

A short calculation shows that V is a first integral for (10). Since level sets of V that are close enough to (x^*, y^*) are closed curves, we obtain that (x^*, y^*) is indeed a center.

We can also deduce the global behavior for $(a_1, b_3) = (0, 0)$ and $a_3 b_1 > 0$. Recall that we defined both the ODE (4) and the function V on the positive quadrant. If $a_3 \leq -1$ and $b_1 \leq -1$, then $V(x, y)$ approaches infinity whenever x or y approaches zero or infinity. Hence, all level sets of V are closed curves, see Figure 2 for the corresponding phase portrait. On the other hand, if at least one of $a_3 > -1$ and $b_1 > -1$ holds, then some level sets intersect the boundary of the positive quadrant. Hence, the level sets of V that are close enough to (x^*, y^*) are still closed curves, but some level sets connect two points on the boundary (or touch the boundary in one point). In Figure 3, we have collected the phase portraits for four cases where at least one of $a_3 \leq -1$ or $b_1 \leq -1$ is violated.

Solutions approaching the boundary forward (respectively, backward) in time either

- reach the boundary in finite time, and thus these solutions are not defined for all positive (respectively, negative) times or
- stay in the positive quadrant for all positive (respectively, negative) times.

Which of the two cases occurs is not determined solely by the values of a_3 and b_1 , but also by the values of α_2 and β_2 .

4.2.4 Asymptotic stability for all k : Theorem 4

Assume $\det C \neq 0$ and let J be the Jacobian matrix at the unique positive equilibrium (x^*, y^*) . Then, by Proposition 2 (i), we have $\operatorname{tr} J \leq 0$ if and only if $a_1 - Kb_3 \leq 0$, where $K = \frac{k_3 x^*}{k_2 y^*}$. We claim that K can take any positive value if either

- the parameters k_1, k_2, k_3, k_4 can take any positive values, or
- the parameters k_1, k_2, k_3, k_4 can take any positive values with $k_2 = nk_3$.

To prove the claim, let k_2, k_3, x^* , and y^* be arbitrary positive numbers (with $k_2 = nk_3$ in the second case). Then the unique positive equilibrium of the ODE (4) with $k_1 = k_2 (x^*)^{-a_1} (y^*)^{-b_2}$ and $k_4 = k_3 (x^*)^{-a_3} (y^*)^{-b_3}$ is indeed (x^*, y^*) . This concludes the proof of the claim.

As a consequence, each of the statements (i) and (ii) in Theorem 4 implies $a_1 \leq 0 \leq b_3$. By Proposition 2 (i), asymptotic stability of the unique positive equilibrium implies $\det C < 0$. By the discussion in Subsection 4.2.3, the unique positive equilibrium is not asymptotically stable if $(a_1, b_3) = (0, 0)$. Thus, each of the statements (i) and (ii) in Theorem 4 implies (iii).

On the other hand, statement (iii) in Theorem 4 implies $\operatorname{tr} J < 0$ and $\det J > 0$. Therefore, both eigenvalues of J have negative real part, and therefore the positive equilibrium is asymptotically stable. Thus, statement (iii) implies both (i) and (ii). This concludes the proof of Theorem 4.

4.3 Global asymptotic stability for all k : Theorem 5

By Theorem 4, the unique positive equilibrium of the ODE (4) is asymptotically stable for all k if and only if $\det C < 0$, $a_1 \leq 0 \leq b_3$, and $(a_1, b_3) \neq (0, 0)$. Theorem 5 states that – apart from some boundary cases – asymptotic stability implies global asymptotic stability. To prove it, we need to rule out periodic solutions, unbounded solutions, and solutions approaching the boundary of the positive quadrant. For the technical analysis, we consider the ODE (5).

4.3.1 Precluding periodic solutions

To preclude periodic solutions, we use the Bendixson-Dulac test. Let $h: \mathbb{R}_+^2 \rightarrow \mathbb{R}_+$ and $(f, g): \mathbb{R}_+^2 \rightarrow \mathbb{R}^2$ be two continuously differentiable functions. Then

$$\frac{\operatorname{div}(hf, hg)}{h} = \operatorname{div}(f, g) + f \frac{\partial_1 h}{h} + g \frac{\partial_2 h}{h} = \partial_1 f + \partial_2 g + f \frac{\partial_1 h}{h} + g \frac{\partial_2 h}{h}.$$

Let $f(x, y) = k_1 x^{a_1} y^{b_1} - k_2$ and $g(x, y) = k_3 - k_4 x^{a_3} y^{b_3}$ denote the right-hand side of the ODE (5) and choose $h(x, y) = x^{-p} y^{-q}$ as Dulac function. Then $\frac{\partial_1 h}{h} = -\frac{p}{x}$, $\frac{\partial_2 h}{h} = -\frac{q}{y}$, and

$$\frac{\operatorname{div}(hf, hg)}{h} = k_1(a_1 - p)x^{a_1-1}y^{b_1} + k_2px^{-1} + k_3(-q)y^{-1} + k_4(q - b_3)x^{a_3}y^{b_3-1}.$$

Thus, if $a_1 \leq 0 \leq b_3$ and $(a_1, b_3) \neq (0, 0)$, and p and q are chosen such that $a_1 \leq p \leq 0 \leq q \leq b_3$, then $\frac{\operatorname{div}(hf, hg)}{h} < 0$ on \mathbb{R}_+^2 . Therefore, by the Bendixson-Dulac test, the ODE (5) does not admit periodic solutions.

4.3.2 Precluding unbounded solutions

In order to prove boundedness of the solutions in the case $a_1 < 0 < b_3$ and $\det C < 0$, we consider all possible signs of a_3 and b_1 and the corresponding nullcline geometries. For phase portraits in the nine cases, see Figure 4. In two cases (top left and bottom right), solutions may spiral around the unique positive equilibrium. Since the divergence of the right-hand side of the ODE (5) is negative, see Subsection 4.3.1, they can spiral inwards only (anti-clockwise and clockwise, respectively). In the other seven cases, solutions are ultimately monotonic.

In the cases $a_1 < 0 = b_3$ and $a_1 = 0 < b_3$, we prove boundedness of the solutions by providing a Lyapunov function. In fact, we use a continuously differentiable function $V: \mathbb{R}_+^2 \rightarrow \mathbb{R}$ defined by Equations (11). Let $f(x, y) = k_1 x^{a_1} y^{b_1} - k_2$ and $g(x, y) = k_3 - k_4 x^{a_3} y^{b_3}$ denote the right-hand side of the ODE (5). The time derivative of V along a solution amounts to

$$\begin{aligned} \dot{V} &= (\partial_1 V) \dot{x} + (\partial_2 V) \dot{y} \\ &= (\partial_1 V) f + (\partial_2 V) g \\ &= x^{a_3} y^{b_1} \cdot \begin{cases} k_1 k_3 [x^{-a_3} - (x^*)^{-a_3}] [x^{a_1} - (x^*)^{a_1}], & \text{if } b_3 = 0, \\ (-k_2 k_4) [y^{-b_1} - (y^*)^{-b_1}] [y^{b_3} - (y^*)^{b_3}], & \text{if } a_1 = 0, \end{cases} \end{aligned}$$

where we use $a_3 b_1 > 0$ (which follows from $\det C < 0$). We first consider $a_3, b_1 < 0$. In both cases, $a_1 < 0 = b_3$ and $a_1 = 0 < b_3$, we obtain that $\dot{V} \leq 0$ in \mathbb{R}_+^2 . Since the sublevel sets of V are bounded subsets of \mathbb{R}_+^2 , the solutions stay bounded forward in time. It remains to consider $a_3, b_1 > 0$. Here, we obtain that $\dot{V} \geq 0$, and the superlevel sets of V are bounded. This concludes the proof of the boundedness of the solutions of the ODE (5).

4.3.3 Solutions approaching the boundary of the positive quadrant

We assume $a_1 \leq 0 \leq b_3$ and $\det C < 0$. We prove that no solution of the ODE (5) approaches the boundary of the positive quadrant if and only if either

- $a_1 < 0 < b_3$,
- $a_1 < 0 = b_3$, $a_3 < 0$, and $b_1 \leq -1$, or
- $a_1 = 0 < b_3$, $a_3 \leq -1$, and $b_1 < 0$.

In the case $a_1 < 0 < b_3$, this follows from the nullcline geometries shown in Figure 4. See the discussion at the beginning of Subsection 4.3.2.

In the cases $a_1 < 0 = b_3$ and $a_1 = 0 < b_3$, $\det C < 0$ implies $a_3 b_1 > 0$. We first consider $a_3, b_1 > 0$ and show that there exist solutions approaching the boundary.

In the case $a_1 < 0 = b_3$ (and $a_3, b_1 > 0$), the vector field is defined even for $y = 0$ and $x > 0$ and points transversally out of the non-negative quadrant for $y = 0$ and $x > x^*$. For the phase portrait, see the top left panel in Figure 5.

In the case $a_1 = 0 < b_3$ (and $a_3, b_1 > 0$), the vector field is defined even for $x = 0$ and $y > 0$ and points transversally out of the non-negative quadrant for $x = 0$ and $0 < y < y^*$. See the top right panel in Figure 5.

It remains to examine the cases

- $a_1 < 0 = b_3$ and $a_3, b_1 < 0$ and
- $a_1 = 0 < b_3$ and $a_3, b_1 < 0$.

In the case $a_1 < 0 = b_3$ (and $a_3, b_1 < 0$), the y -axis is repelling. If additionally $b_1 \leq -1$ then the level sets of the Lyapunov function V defined by Equations (11) are disjoint from the x -axis, and therefore no solution can approach the x -axis either. For the phase portrait, see the middle left panel in Figure 5. If alternatively $-1 < b_1 < 0$ then we show that some of the solutions approach the x -axis. Consider the auxiliary ODE

$$\begin{aligned}\dot{x} &= k_1 x^{a_1} y^{b_1}, \\ \dot{y} &= k_3 - k_4 x^{a_3}\end{aligned}\tag{12}$$

in the positive quadrant. Since the ODE (12) is separable, one can solve it explicitly. We are particularly interested in a solution that approaches the boundary of the positive quadrant at the point $(x^*, 0)$. The orbit of such a solution is given by the curve

$$y = \left[\frac{(b_1 + 1)}{k_1} \left(k_3 \frac{x^{1-a_1} - (x^*)^{1-a_1}}{1-a_1} - k_4 \frac{x^{1+a_3-a_1} - (x^*)^{1+a_3-a_1}}{1+a_3-a_1} \right) \right]^{\frac{1}{b_1+1}}$$

for $0 < x < x^*$ if $1 + a_3 - a_1 \neq 0$ and

$$y = \left[\frac{(b_1 + 1)}{k_1} \left(k_3 \frac{x^{1-a_1} - (x^*)^{1-a_1}}{1-a_1} - k_4 (\ln x - \ln x^*) \right) \right]^{\frac{1}{b_1+1}}$$

for $0 < x < x^*$ if $1 + a_3 - a_1 = 0$. In any case, the unique positive equilibrium (x^*, y^*) of the ODE (5) lies to the right of this curve, and solutions of the ODE (5) that start on or to the left of the curve approach the x -axis at a point $(\tilde{x}, 0)$ with $0 < \tilde{x} \leq x^*$. For the phase portrait, see the bottom left panel in Figure 5, and for the construction of the curve and the resulting forward invariant set of the ODE (5), see the left panel in Figure 6.

In case $a_1 = 0 < b_3$ (and $a_3, b_1 < 0$), the x -axis is repelling. If additionally $a_3 \leq -1$, then the level sets of the Lyapunov function V are disjoint from the y -axis, and therefore no solution can approach the y -axis either. For the phase portrait, see the middle right panel in Figure 5. If alternatively $-1 < a_3 < 0$ then

we show that some of the solutions approach the y -axis. Consider the auxiliary ODE

$$\begin{aligned}\dot{x} &= k_1 y^{b_1} - k_2, \\ \dot{y} &= -k_4 x^{a_3} y^{b_3}\end{aligned}\tag{13}$$

in the positive quadrant. Since the ODE (13) is separable, one can solve it explicitly. We are particularly interested in a solution that approaches the boundary of the positive quadrant at the point $(0, y^*)$. The orbit of such a solution is given by the curve

$$x = \left[-\frac{(a_3 + 1)}{k_4} \left(k_1 \frac{y^{1+b_1-b_3} - (y^*)^{1+b_1-b_3}}{1+b_1-b_3} - k_2 \frac{y^{1-b_3} - (y^*)^{1-b_3}}{1-b_3} \right) \right]^{\frac{1}{a_3+1}}$$

for $y > y^*$ if $1 + b_1 - b_3 \neq 0$ and $b_3 \neq 1$,

$$x = \left[-\frac{(a_3 + 1)}{k_4} \left(k_1 (\ln y - \ln y^*) - k_2 \frac{y^{1-b_3} - (y^*)^{1-b_3}}{1-b_3} \right) \right]^{\frac{1}{a_3+1}}$$

for $y > y^*$ if $1 + b_1 - b_3 = 0$, and

$$x = \left[-\frac{(a_3 + 1)}{k_4} \left(k_1 \frac{y^{b_1} - (y^*)^{b_1}}{b_1} - k_2 (\ln y - \ln y^*) \right) \right]^{\frac{1}{a_3+1}}$$

for $y > y^*$ if $b_3 = 1$. In any case, the unique positive equilibrium (x^*, y^*) of the ODE (5) lies below this curve, and solutions of the ODE (5) that start on or above the curve approach the y -axis at a point $(0, \tilde{y})$ with $\tilde{y} \geq y^*$. For the phase portrait, see the bottom right panel in Figure 5, and for the construction of the curve and the resulting forward invariant set of the ODE (5), see the right panel in Figure 6.

This concludes the proof of Theorem 5.

4.4 Preclusion of global stability: Proposition 6

We assume $\det C < 0$ and $(a_1, b_3) \neq (0, 0)$. The unique positive equilibrium (x^*, y^*) is asymptotically stable (respectively, repelling) if $a_1 \leq 0 \leq b_3$ (respectively, if $a_1 \geq 0 \geq b_3$), since the trace of the Jacobian matrix at (x^*, y^*) is negative (respectively, positive), see Proposition 2.

Proposition 6 deals with the cases $a_1, b_3 < 0$ and $a_1, b_3 > 0$. In both cases, $\det C < 0$ implies $a_3 b_1 > 0$. In each of the four subcases in Proposition 6, we construct a closed forward invariant set that does not contain the unique positive equilibrium, see Figure 7.

We prove the four statements in Proposition 6 separately, see Lemmas 11, 12, 13, and 14 below. In order to ease the notation in the proofs of these lemmas, we consider the ODE (5) with $k_1 = k_2 = k_3 = k_4 = 1$, that is,

$$\begin{aligned}\dot{x} &= x^{a_1} y^{b_1} - 1, \\ \dot{y} &= 1 - x^{a_3} y^{b_3}.\end{aligned}\tag{14}$$

However, the assumption $k_1 = k_2 = k_3 = k_4 = 1$ is not necessary for the validity of the lemmas.

Lemma 11 Assume $a_1 < 0$, $b_1 < 0$, $a_3 < 0$, $b_3 < 0$, and $\det C < 0$. If

$$1 + b_1 - b_3 > 0 \quad \text{or} \quad \det C > a_3 + b_3,$$

then there exist $\gamma < -\frac{a_3}{b_3}$ and $x_0 > 1$ such that the set

$$\{(x, y) \in \mathbb{R}_+^2 \mid x \geq x_0 \text{ and } 0 < y \leq x^\gamma\}$$

is forward invariant under the ODE (14). (See the top left panel in Figure 7.)

Proof We want to find $\gamma < -\frac{a_3}{b_3}$ and $x_0 > 1$ such that, along the curve $y = x^\gamma$,

$$\frac{dy}{dx} = \frac{\dot{y}}{\dot{x}} = \frac{1 - x^{a_3}(x^\gamma)^{b_3}}{x^{a_1}(x^\gamma)^{b_1} - 1} < \gamma x^{\gamma-1} = \frac{dx^\gamma}{dx} \quad \text{for all } x \geq x_0$$

or, equivalently,

$$\gamma^{-1} x^{1-\gamma} \frac{1 - x^{a_3+\gamma b_3}}{x^{a_1+\gamma b_1} - 1} > 1 \quad \text{for all } x \geq x_0.$$

The assumptions imply $-\frac{a_3}{b_3} < -\frac{a_1}{b_1} < 0$, and $\gamma < -\frac{a_3}{b_3}$ further implies $a_3 + \gamma b_3 > 0$ and $a_1 + \gamma b_1 > 0$. Hence,

$$\lim_{x \rightarrow \infty} \gamma^{-1} x^{1-\gamma} \frac{1 - x^{a_3+\gamma b_3}}{x^{a_1+\gamma b_1} - 1} = \lim_{x \rightarrow \infty} -\gamma^{-1} x^{(1-a_1+a_3)-\gamma(1+b_1-b_3)} = \infty,$$

if additionally

$$(1 - a_1 + a_3) - \gamma(1 + b_1 - b_3) > 0.$$

If $1 + b_1 - b_3 > 0$, we just choose $-\gamma$ large enough. If $\det C > a_3 + b_3$, a short calculation shows $(1 - a_1 + a_3) + \frac{a_3}{b_3}(1 + b_1 - b_3) > 0$. Hence, if $1 + b_1 - b_3 = 0$, the above inequality holds (for every γ), and if $1 + b_1 - b_3 < 0$, we obtain

$$\frac{1 - a_1 + a_3}{1 + b_1 - b_3} < -\frac{a_3}{b_3}$$

and choose γ between the left- and right-hand side of the last inequality. \square

Lemma 12 Assume $a_1 < 0$, $b_1 > 0$, $a_3 > 0$, $b_3 < 0$, and $\det C < 0$. If

$$\det C > a_3 + b_3,$$

then there exist $\gamma > -\frac{a_3}{b_3}$ and $x_0 > 1$ such that the set

$$\{(x, y) \in \mathbb{R}_+^2 \mid x \geq x_0 \text{ and } x^\gamma \leq y\}$$

is forward invariant under the ODE (14). (See the top right panel in Figure 7.)

Proof We want to find $\gamma > -\frac{a_3}{b_3}$ and $x_0 > 1$ such that, along the curve $y = x^\gamma$,

$$\frac{dy}{dx} = \frac{\dot{y}}{\dot{x}} = \frac{1 - x^{a_3}(x^\gamma)^{b_3}}{x^{a_1}(x^\gamma)^{b_1} - 1} > \gamma x^{\gamma-1} = \frac{dx^\gamma}{dx} \quad \text{for all } x \geq x_0$$

or, equivalently,

$$\gamma^{-1} x^{1-\gamma} \frac{1 - x^{a_3+\gamma b_3}}{x^{a_1+\gamma b_1} - 1} > 1 \quad \text{for all } x \geq x_0.$$

The assumptions imply $0 < -\frac{a_1}{b_1} < -\frac{a_3}{b_3}$, and $\gamma > -\frac{a_3}{b_3}$ further implies $a_3 + \gamma b_3 < 0$ and $a_1 + \gamma b_1 > 0$. Hence,

$$\lim_{x \rightarrow \infty} \gamma^{-1} x^{1-\gamma} \frac{1 - x^{a_3+\gamma b_3}}{x^{a_1+\gamma b_1} - 1} = \lim_{x \rightarrow \infty} \gamma^{-1} x^{(1-a_1)-\gamma(1+b_1)} = \infty,$$

if additionally

$$(1 - a_1) - \gamma(1 + b_1) > 0.$$

If $\det C > a_3 + b_3$, then $(1 - a_1) + \frac{a_3}{b_3}(1 + b_1) > 0$. Hence, we obtain

$$-\frac{a_3}{b_3} < \frac{1 - a_1}{1 + b_1}$$

and choose γ between the left- and right-hand side of the last inequality. \square

Lemma 13 Assume $a_1 > 0$, $b_1 > 0$, $a_3 > 0$, $b_3 > 0$, and $\det C < 0$. Then for all $-\frac{a_1}{b_1} < \gamma < 0$ there exists $0 < x_0 < 1$ such that the set

$$\{(x, y) \in \mathbb{R}_+^2 \mid 0 < x \leq x_0 \text{ and } x_0^\gamma \leq y \leq x^\gamma\}$$

is forward invariant under the ODE (14). (See the bottom left panel in Figure 7.)

Proof Fix $-\frac{a_1}{b_1} < \gamma < 0$. We claim that there exists $0 < x_0 < 1$ such that, along the curve $y = x^\gamma$,

$$\frac{dy}{dx} = \frac{\dot{y}}{\dot{x}} = \frac{1 - x^{a_3}(x^\gamma)^{b_3}}{x^{a_1}(x^\gamma)^{b_1} - 1} > \gamma x^{\gamma-1} = \frac{dx^\gamma}{dx} \quad \text{for all } x \geq x_0$$

or, equivalently,

$$\gamma^{-1} x^{1-\gamma} \frac{1 - x^{a_3+\gamma b_3}}{x^{a_1+\gamma b_1} - 1} < 1 \quad \text{for all } 0 < x \leq x_0.$$

The assumptions imply $-\frac{a_3}{b_3} < -\frac{a_1}{b_1} < 0$, and $-\frac{a_1}{b_1} < \gamma < 0$ further implies $a_3 + \gamma b_3 > 0$ and $a_1 + \gamma b_1 > 0$. Hence,

$$\lim_{x \rightarrow 0} \gamma^{-1} x^{1-\gamma} \frac{1 - x^{a_3+\gamma b_3}}{x^{a_1+\gamma b_1} - 1} = \lim_{x \rightarrow 0} -\gamma^{-1} x^{1-\gamma} = 0.$$

\square

Lemma 14 Assume $a_1 > 0$, $b_1 < 0$, $a_3 < 0$, $b_3 > 0$, and $\det C < 0$. If

$$1 - a_1 < 0 \quad \text{or} \quad a_1 + b_1 > 0,$$

then there exist $0 < \gamma < -\frac{a_1}{b_1}$ and $x_0 > 1$ such that the set

$$\{(x, y) \in \mathbb{R}_+^2 \mid x \geq x_0 \text{ and } x_0^\gamma \leq y \leq x^\gamma\}$$

is forward invariant under the ODE (14). (See the bottom right panel in Figure 7.)

Proof We want to find $0 < \gamma < -\frac{a_1}{b_1}$ and $x_0 > 1$ such that, along the curve $y = x^\gamma$,

$$\frac{dy}{dx} = \frac{\dot{y}}{\dot{x}} = \frac{1 - x^{a_3}(x^\gamma)^{b_3}}{x^{a_1}(x^\gamma)^{b_1} - 1} < \gamma x^{\gamma-1} \frac{dx^\gamma}{dx} \quad \text{for all } x \geq x_0$$

or, equivalently,

$$\gamma^{-1} x^{1-\gamma} \frac{1 - x^{a_3+\gamma b_3}}{x^{a_1+\gamma b_1} - 1} < 1 \quad \text{for all } x \geq x_0.$$

The assumptions imply $0 < -\frac{a_1}{b_1} < -\frac{a_3}{b_3}$, and $0 < \gamma < -\frac{a_1}{b_1}$ further implies $a_3 + \gamma b_3 < 0$ and $a_1 + \gamma b_1 > 0$. Hence,

$$\lim_{x \rightarrow \infty} \gamma^{-1} x^{1-\gamma} \frac{1 - x^{a_3+\gamma b_3}}{x^{a_1+\gamma b_1} - 1} = \lim_{x \rightarrow \infty} \gamma^{-1} x^{(1-a_1)-\gamma(1+b_1)} = 0,$$

if additionally

$$(1 - a_1) - \gamma(1 + b_1) < 0.$$

If $1 - a_1 < 0$, we just choose γ small enough. If $a_1 + b_1 > 0$, a short calculation shows $(1 - a_1) + \frac{a_1}{b_1}(1 + b_1) < 0$. Hence, if $1 + b_1 = 0$, the above inequality holds (for every γ), and if $1 + b_1 > 0$, we obtain

$$\frac{1 - a_1}{1 + b_1} < -\frac{a_1}{b_1}$$

and choose γ between the left- and right-hand side of the last inequality. \square

4.5 Global asymptotic stability for a particular k : Theorem 7

We consider the ODE

$$\begin{aligned} \dot{x} &= x^\alpha - xy^\beta, \\ \dot{y} &= xy^\beta - y \end{aligned} \tag{15}$$

and assume $\alpha\beta - \alpha + 1 \neq 0$.

4.5.1 Local behavior: Theorem 7 (i), (ii), (iii), and (iv)

Most of the statements in Theorem 7 are direct consequences of the results for the ODE (4) with $\alpha_1 = \alpha$, $\beta_1 = 0$, $\alpha_2 = 1$, $\beta_2 = \beta$, $\alpha_3 = 0$, $\beta_3 = 1$, and hence

$$C = \begin{pmatrix} a_1 & b_1 \\ a_3 & b_3 \end{pmatrix} = \begin{pmatrix} \alpha - 1 & -\beta \\ -1 & 1 - \beta \end{pmatrix},$$

and $k_1 = k_2 = k_3 = k_4 = 1$.

Theorem 7 (i) follows from Proposition 1 (i) and Proposition 2 (i). To prove Theorem 7 (iii), we apply Proposition 3. The determinant of the Jacobian matrix at $(1, 1)$ is given by $\alpha\beta - \alpha + 1$, and its trace amounts to $\alpha + \beta - 2$. For vanishing trace, we obtain

$$d_1 = -[(1 - \alpha)(-\beta)(1 - \beta) - (\alpha - 1)(-1)0] = (\alpha - 1)^2(\alpha - 2).$$

Since pairs (α, β) with $\alpha + \beta - 2 = 0$ and $\alpha\beta - \alpha + 1 > 0$ lie on the line segment between $\left(\frac{1-\sqrt{5}}{2}, \frac{3+\sqrt{5}}{2}\right)$ and $\left(\frac{1+\sqrt{5}}{2}, \frac{3-\sqrt{5}}{2}\right)$, we find $\alpha < 2$. Hence, if $(\alpha, \beta) \neq (1, 1)$, then $d_1 < 0$, the equilibrium $(1, 1)$ is asymptotically stable, and the corresponding Andronov-Hopf bifurcation is supercritical. Now, Theorem 7 (ii) follows from Proposition 2 (ii) and Theorem 7 (iii). Finally, we consider $(\alpha, \beta) = (1, 1)$, and hence $a_1 = b_3 = 0$ and $a_3 = b_1 = -1$. Theorem 7 (iv) is a direct consequence of the discussion in Subsection 4.2.3.

4.5.2 Global behavior: Theorem 7 (v)

It remains to characterize the global asymptotic stability of the unique positive equilibrium $(1, 1)$. We assume $\alpha\beta - \alpha + 1 > 0$, a necessary condition for local asymptotic stability.

If $\alpha \leq 1$, $\beta \leq 1$, and $(\alpha, \beta) \neq (1, 1)$, then Theorem 5 implies global asymptotic stability. Indeed, for $\alpha, \beta < 1$ we have $a_1 < 0 < b_3$, for $\alpha < 1 = \beta$ we have $a_1 < 0 = b_3$, $a_3 < 0$, $b_1 \leq -1$, and for $\beta < 1 = \alpha$ we have $a_1 = 0 < b_3$, $a_3 \leq -1$, $b_1 < 0$. (In the latter case, $\beta > 0$ since $\alpha\beta - \alpha + 1 > 0$ and $\alpha = 1$.)

If $\alpha \geq 1$ and $\beta \geq 1$, then we do not even have local asymptotic stability, see Theorem 7 (ii).

If $\alpha < 1$ and $\beta > 1$ then Lemma 11 precludes global asymptotic stability. Indeed, we have $a_1 = \alpha - 1 < 0$, $b_1 = -\beta < 0$, $a_3 = -1 < 0$, $b_3 = 1 - \beta < 0$, and

$$\det C - (a_3 + b_3) = -\alpha\beta + \alpha - 1 + \beta = (1 - \alpha)(\beta - 1) > 0.$$

If $\alpha > 1$, $\beta < 1$, and $\beta < \alpha - 1$ then Lemma 14 precludes global asymptotic stability. Indeed, we have $a_1 = \alpha - 1 > 0$, $b_1 = -\beta < 0$ (since $\alpha\beta - \alpha + 1 > 0$ and $\alpha > 1$), $a_3 = -1 < 0$, $b_3 = 1 - \beta > 0$, and $a_1 + b_1 = \alpha - 1 - \beta > 0$.

It remains to consider the case $\alpha > 1$ and $\alpha - 1 \leq \beta < 1$. Now, if $\beta > 2 - \alpha$, then the trace of the Jacobian matrix at $(1, 1)$ is positive, and we do not even have local asymptotic stability. Therefore, for the rest of this section, we assume

$$1 < \alpha \leq \frac{3}{2} \text{ and } \alpha - 1 \leq \beta \leq 2 - \alpha \quad (16)$$

and show that the equilibrium $(1, 1)$ is globally asymptotically stable in this region of the (α, β) -plane, see the light green triangle in Figure 1.

For the exponents in the x -nullcline $y = x^{\frac{\alpha-1}{\beta}}$ and the y -nullcline $y = x^{\frac{1}{1-\beta}}$, the assumptions (16) imply $0 < \frac{\alpha-1}{\beta} \leq 1 < \frac{1}{1-\beta}$. For a typical phase portrait, see Figure 8.

Note that a solution can approach the boundary only at the origin. Indeed, the x -axis for $x > 0$ is repelling, while the y -axis for $y > 0$ is an orbit (if we extend the state space of the ODE from the positive quadrant to the non-negative quadrant), and solutions starting at $(0, y_0)$ with $y_0 > 0$ are unique backward in time.

To prove global asymptotic stability, we have to show that no solution starting in the positive quadrant

- approaches the origin,
- is unbounded or
- periodic.

This is guaranteed by the following three results. In Lemma 15, we construct a Dulac function which allows to rule out periodic solutions by the Bendixson-Dulac test. Lemma 16 ensures that all orbits are bounded, and Lemma 17 precludes convergence to the origin.

Lemma 15 *Let $f(x, y) = x^\alpha - xy^\beta$ and $g(x, y) = xy^\beta - y$ denote the right-hand side of the ODE (15), and let J be the Jacobian matrix at $(1, 1)$. Assume (16) and let*

$$h(x, y) = x^{-p}y^{-q} \text{ with } p = \alpha - \frac{(\alpha-1)\beta}{\det J}, q = \beta + \frac{(\alpha-1)^2\beta}{\det J}$$

and $v = \frac{\operatorname{div}(hf, hg)}{h}$. Then, for $(x, y) \in \mathbb{R}_+^2$,

$$\begin{aligned} v(x, y) &< v(1, 1) < 0 \text{ for } (x, y) \neq (1, 1), & \text{if } 1 < \alpha < \frac{3}{2} \text{ and } \alpha - 1 < \beta < 2 - \alpha, \\ v(x, y) &< v(1, 1) = 0 \text{ for } (x, y) \neq (1, 1), & \text{if } 1 < \alpha < \frac{3}{2} \text{ and } \beta = 2 - \alpha, \\ v(x, y) &< v(1, 1) < 0 \text{ for } x \neq y, & \text{if } 1 < \alpha < \frac{3}{2} \text{ and } \alpha - 1 = \beta, \\ v(x, y) &< v(1, 1) = 0 \text{ for } x \neq y, & \text{if } \alpha = \frac{3}{2} \text{ and } \beta = \frac{1}{2}. \end{aligned}$$

Proof We first explain the choice of p and q in the definition of h . Since

$$v = \frac{\operatorname{div}(hf, hg)}{h} = \partial_1 f + \partial_2 g + f \frac{\partial_1 h}{h} + g \frac{\partial_2 h}{h},$$

we have $v(1, 1) = \operatorname{tr} J$. Hence, for $\operatorname{tr} J = \alpha + \beta - 2 = 0$ (at the supercritical Andronov-Hopf bifurcation), we have $v \leq 0$ on \mathbb{R}_+^2 only if v has a local maximum at $(1, 1)$. A short calculation shows that $(\operatorname{grad} v)(1, 1) = (0, 0)$ uniquely determines p and q . For $\alpha + \beta - 2 < 0$, other p and q may also be appropriate.

We now turn to the proof of the lemma. We assume (16) and find

$$\begin{aligned} v(x, y) &= (\alpha - p)x^{\alpha-1} + (p - 1)y^\beta + (\beta - q)xy^{\beta-1} + q - 1 \quad \text{and} \\ (\partial_1 v)(x, y) &= (\alpha - p)(\alpha - 1)x^{\alpha-2} + (\beta - q)y^{\beta-1} \\ &= \frac{(\alpha - 1)^2\beta}{\det J}(x^{\alpha-2} - y^{\beta-1}), \end{aligned}$$

where $\frac{(\alpha-1)^2\beta}{\det J} > 0$.

For fixed $y > 0$, the function $x \mapsto v(x, y)$ has its maximum at $x = y^{\frac{1-\beta}{2-\alpha}}$ and

$$\max_{(x,y) \in \mathbb{R}_+^2} v(x, y) = \max_{y>0} \tilde{v}(y) \quad \text{with } \tilde{v}(y) = v\left(y^{\frac{1-\beta}{2-\alpha}}, y\right).$$

We find

$$\begin{aligned} \tilde{v}(y) &= (\alpha - p + \beta - q)y^{\frac{(\alpha-1)(1-\beta)}{2-\alpha}} + (p-1)y^\beta + q - 1 \\ &= \frac{(\alpha-1)(2-\alpha)\beta}{\det J} y^{\frac{(\alpha-1)(1-\beta)}{2-\alpha}} - \frac{(\alpha-1)^2(1-\beta)}{\det J} y^\beta + q - 1 \quad \text{and} \\ \tilde{v}'(y) &= \frac{(\alpha-1)^2\beta(1-\beta)}{\det J} \left(y^{\frac{(\alpha-1)(1-\beta)}{2-\alpha}-1} - y^{\beta-1} \right), \end{aligned}$$

where $\frac{(\alpha-1)^2\beta(1-\beta)}{\det J} > 0$.

If $\beta > \alpha - 1$, then $\frac{(\alpha-1)(1-\beta)}{2-\alpha} - 1 < \beta - 1$ and hence $\tilde{v}(y) < v(1, 1)$ for all $y > 0$.
If $\beta = \alpha - 1$, then $\frac{(\alpha-1)(1-\beta)}{2-\alpha} - 1 = \beta - 1$ and hence $v(y, y) = v(1, 1)$ for all $y > 0$ and $v(x, y) < v(1, 1)$ for $x \neq y$. \square

Lemma 16 *Assume (16). Then all solutions of the ODE (15) starting in the positive quadrant are bounded.*

Proof We claim that solutions of the ODE (15) starting below the x -nullcline with $x > 1$ eventually cross it, see the left panel in Figure 9. Solutions above the x -nullcline with $x > 1$ eventually cross the y -nullcline after which y decreases, see Figure 8. Since orbits spiraling outwards are precluded by Lemma 15, all orbits are bounded.

To prove our claim, we consider a starting point below the x -nullcline and show that there exists a curve below the point on which the vector field points upward and which eventually intersects the x -nullcline. Formally, we show that there exists c_0 with $0 < c_0 < 1$ such that for all c with $0 < c \leq c_0$ the following statement holds. Along the curve $y = cx^{\frac{1}{1-\beta}}$,

$$\frac{dy}{dx} = \frac{\dot{y}}{\dot{x}} = \frac{g(x, cx^{\frac{1}{1-\beta}})}{f(x, cx^{\frac{1}{1-\beta}})} > \frac{c}{1-\beta} x^{\frac{1}{1-\beta}-1} = \frac{d}{dx} cx^{\frac{1}{1-\beta}} \quad \text{for all } 0 < x < c^{-\frac{\beta(1-\beta)}{\det J}},$$

where $f(x, y) = x^\alpha - xy^\beta$ and $g(x, y) = xy^\beta - y$ denote the right-hand side of the ODE (15).

The assumptions (16) imply $0 < \frac{\alpha-1}{\beta} \leq 1 < \frac{1}{1-\beta}$. Hence, the x -nullcline $y = x^{\frac{\alpha-1}{\beta}}$ and the scaled y -nullcline $y = cx^{\frac{1}{1-\beta}}$ intersect at $x = 0$ and $x = c^{-\frac{\beta(1-\beta)}{\det J}}$.

A short calculation shows that the statement in question is equivalent to

$$p(x) > 0 \quad \text{for all } 0 < x < c^{-\frac{\beta(1-\beta)}{\det J}}$$

with

$$p(x) = x^{\frac{\beta}{1-\beta}} - x^{\alpha-1}c^{-\beta} + (1-\beta)(c^{-1} - c^{-\beta}).$$

The function p has its minimum at

$$\bar{x} = \left(\frac{\beta - \det J}{\beta} \right)^{\frac{1-\beta}{\det J}} c^{-\frac{\beta(1-\beta)}{\det J}},$$

where $0 < \bar{x} < c^{-\frac{\beta(1-\beta)}{\det J}}$ since $\det J < \beta$. We find

$$p(\bar{x}) = -\frac{\det J}{\beta - \det J} \left(\frac{\beta - \det J}{\beta} \right)^{\frac{\beta}{\det J}} c^{-\frac{\beta^2}{\det J}} + (1 - \beta)(c^{-1} - c^{-\beta}),$$

where the first summand is negative and the second summand is positive.

If $\beta > \alpha - 1$, then $-\frac{\beta^2}{\det J} > -1$. Therefore, $p(\bar{x}) \rightarrow \infty$ as $c \rightarrow 0$. If $\beta = \alpha - 1$, then $\det J = \beta^2$. Therefore,

$$p(\bar{x}) = \left(-\beta(1 - \beta)^{\frac{1}{\beta}-1} + (1 - \beta) \right) c^{-1} - (1 - \beta)c^{-\beta},$$

where the first summand is positive since $0 < \beta \leq \frac{1}{2}$, and $p(\bar{x}) \rightarrow \infty$ as $c \rightarrow 0$. \square

Lemma 17 *Assume (16). Then no solution of the ODE (15) starting in the positive quadrant approaches the origin.*

Proof We show that solutions of the ODE (15) starting above the x -nullcline with $y > 0$ small enough eventually cross it, see the right panel in Figure 9.

Fix $\gamma > \frac{\alpha-1}{\beta}$. Every starting point (x_0, y_0) above the x -nullcline $y = x^{\frac{\alpha-1}{\beta}}$ with $y_0 > 0$ small enough lies on a curve $y = cx^\gamma$ with $c > 1$ on which the vector field points downward and which eventually intersects the x -nullcline. Indeed, the intersection occurs at $x = c^{-1/(\gamma - \frac{\alpha-1}{\beta})}$ with $c = y_0/x_0^\gamma$. Finally, we prove that, along any curve $y = cx^\gamma$ with $c > 1$,

$$\frac{dy}{dx} = \frac{\dot{y}}{\dot{x}} = \frac{xy^\beta - y}{x^\alpha - xy^\beta} > \gamma \frac{y}{x} = \frac{d}{dx} cx^\gamma \quad \text{for all } x^{\frac{\alpha-1}{\beta}} < y < \min(1, \gamma^{-\frac{1}{\beta}})$$

or, equivalently,

$$h(x, y) < 1 - \gamma y^\beta \quad \text{for all } x^{\frac{\alpha-1}{\beta}} < y < \min(1, \gamma^{-\frac{1}{\beta}})$$

with

$$h(x, y) = xy^{\beta-1} - \gamma x^{\alpha-1}.$$

We have

$$\begin{aligned} h(0, y) &= 0 < 1 - \gamma y^\beta, & \text{if } 0 < y < \gamma^{-\frac{1}{\beta}} \quad \text{and} \\ h(y^{\frac{\beta}{\alpha-1}}, y) &= y^{\frac{\beta}{\alpha-1} + \beta - 1} - \gamma y^\beta < 1 - \gamma y^\beta, & \text{if } 0 < y < 1. \end{aligned}$$

Since the function $x \mapsto h(x, y)$ is convex for $1 < \alpha < 2$, we obtain $h(x, y) < 1 - \gamma y^\beta$ if $0 < x < y^{\frac{\beta}{\alpha-1}}$ and $0 < y < \min(1, \gamma^{-\frac{1}{\beta}})$. \square

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References

1. A. A. Andronov and E. A. Leontovich. Some cases of dependence of limit cycles on a parameter. *Uchenye zapiski Gorkovskogo Universiteta*, 6:3–24, 1937.
2. A. A. Andronov, E. A. Leontovich, I. I. Gordon, and A. G. Maier. *Theory of bifurcations of dynamic systems on a plane*. Halsted Press [A division of John Wiley & Sons], New York-Toronto, Ont.; Israel Program for Scientific Translations, Jerusalem-London, 1973. Translated from the Russian.
3. A. Dancsó, H. Farkas, M. Farkas, and G. Szabó. Investigations into a class of generalized two-dimensional Lotka-Volterra schemes. *Acta Appl. Math.*, 23(2):103–127, 1991.
4. H. Farkas and Z. Noszticzius. Generalized Lotka-Volterra schemes and the construction of two-dimensional explodator cores and their Liapunov functions via “critical” Hopf bifurcations. *J. Chem. Soc. Faraday Trans. II*, 81(10):1487–1505, 1985.
5. M. Farkas. *Periodic Motions*, volume 104 of *Applied Mathematical Sciences*. Springer-Verlag, New York, 1994.
6. M. Frommer. Über das Auftreten von Wirbeln und Strudeln (geschlossener und spiraler Integralkurven) in der Umgebung rationaler Unbestimmtheitsstellen. *Math. Ann.*, 109(1):395–424, 1934.
7. J. Guckenheimer and P. Holmes. *Nonlinear oscillations, dynamical systems, and bifurcations of vector fields*, volume 42 of *Applied Mathematical Sciences*. Springer-Verlag, New York, 1990. Revised and corrected reprint of the 1983 original.
8. E. Hopf. Abzweigung einer periodischen Lösung von einer stationären Lösung eines Differentialsystems. *Ber. Sächs. Akad. Wiss. Leipzig, Math.-Phys. Kl.*, 94:1–22, 1942.
9. J. Llibre. A counterexample to a result on Lotka-Volterra systems. *Acta Applicandae Mathematicae*, 142(1):123–125, 2016.
10. A. J. Lotka. Contribution to the theory of periodic reactions. *J. Phys. Chem.*, 14(3):271–274, 1910.
11. A. J. Lotka. Analytical note on certain rhythmic relations in organic systems. *Proc. Natl. Acad. Sci.*, 6(7):410–415, 1920.
12. A. J. Lotka. Undamped oscillations derived from the law of mass action. *J. Am. Chem. Soc.*, 42:1595–1599, 1920.
13. S. Müller and G. Regensburger. Generalized mass action systems: Complex balancing equilibria and sign vectors of the stoichiometric and kinetic-order subspaces. *SIAM J. Appl. Math.*, 72:1926–1947, 2012.
14. S. Müller and G. Regensburger. Generalized mass-action systems and positive solutions of polynomial equations with real and symbolic exponents. In V. P. Gerdt, W. Koepf, E. W. Mayr, and E. H. Vorozhtsov, editors, *Computer Algebra in Scientific Computing. Proceedings of the 16th International Workshop (CASC 2014)*, volume 8660 of *Lecture Notes in Comput. Sci.*, pages 302–323, Berlin/Heidelberg, 2014. Springer.
15. W. Yin and E. O. Voit. Construction and customization of stable oscillation models in biology. *Journal of Biological Systems*, 16(04):463–478, 2008.

Appendix A: First focal value

At an Andronov-Hopf bifurcation of a planar ODE, the Jacobian matrix has zero trace and positive determinant.

For a planar ODE

$$\begin{aligned}\dot{x} &= f(x, y), \\ \dot{y} &= g(x, y)\end{aligned}\tag{17}$$

with equilibrium at the origin and Jacobian matrix in normal form,

$$J = \begin{pmatrix} 0 & -\omega \\ \omega & 0 \end{pmatrix},$$

the first focal value (erste Strudelgröße, cf. [6]), called D_1 here, is given by

$$16D_1 = f_{30} + f_{12} + g_{21} + g_{03} + \frac{1}{\omega} [f_{11}(f_{20} + f_{02}) - g_{11}(g_{20} + g_{02}) - f_{20}g_{20} + f_{02}g_{02}], \quad (18)$$

where $f_{30} = (\partial^3 f / \partial x^3)$, $f_{12} = (\partial^3 f / \partial x \partial y^2)$, etc. See, for example, [2, p. 252, eqn. (71)], [5, p. 431, Lemma 7.2.7], or [7, p. 152, eqn. (3.4.11)].

For the planar ODE (17) with equilibrium at the origin and Jacobian matrix

$$J = \begin{pmatrix} a & b \\ c & -a \end{pmatrix},$$

we define the linear transformation

$$\begin{pmatrix} \tilde{x} \\ \tilde{y} \end{pmatrix} = T \begin{pmatrix} x \\ y \end{pmatrix} \quad \text{with} \quad T = \begin{pmatrix} 1 & 0 \\ -\frac{a}{\omega} & -\frac{b}{\omega} \end{pmatrix}$$

and $\omega = \sqrt{\det J} = \sqrt{-a^2 - bc}$. Introducing $h: (x, y)^\top \mapsto (f(x, y), g(x, y))^\top$, we obtain the transformed ODE system

$$\begin{pmatrix} \tilde{x} \\ \tilde{y} \end{pmatrix}^\cdot = T \begin{pmatrix} x \\ y \end{pmatrix}^\cdot = T h \begin{pmatrix} x \\ y \end{pmatrix} = T h \left(T^{-1} \begin{pmatrix} \tilde{x} \\ \tilde{y} \end{pmatrix} \right)$$

with Jacobian matrix $\tilde{J} = T J T^{-1}$ in normal form. Using (18), we compute the first focal value D_1 of the transformed system expressed in terms of derivatives of the original system. We obtain

$$16b^2\omega^2 D_1 = b \left\{ \omega^2 [-2a(f_{21} + g_{12}) + b(f_{30} + g_{21}) - c(f_{12} + g_{03})] + ab \left[+f_{20}^2 - f_{20}g_{11} - f_{11}g_{20} - g_{20}g_{02} - 2g_{11}^2 \right] + ac \left[-f_{20}f_{02} - 2f_{11}^2 - f_{11}g_{02} - f_{02}g_{11} + g_{02}^2 \right] + (bc - 2a^2)[f_{20}f_{11} - g_{11}g_{02}] + b^2g_{20}(f_{20} + g_{11}) - c^2f_{02}(f_{11} + g_{02}) \right\}, \quad (19)$$

See again [2, p. 253, eqn. (76)], where series coefficients are used instead of partial derivatives.

If the equilibrium under consideration differs from the origin, then the derivatives need to be evaluated at the equilibrium.

Appendix B: Figures

In order to illustrate our analysis of the ODE (4) in Section 4, we present phase portraits and figures of forward invariant sets. Thereby, the red curve is the x -nullcline, $x^{a_1}y^{b_1} = \frac{k_2}{k_1}$, while the green curve is the y -nullcline, $x^{a_3}y^{b_3} = \frac{k_3}{k_4}$.

$$\begin{aligned} a_1 &= 0 = b_3, \\ a_3 &\leq -1, b_1 \leq -1 \end{aligned}$$

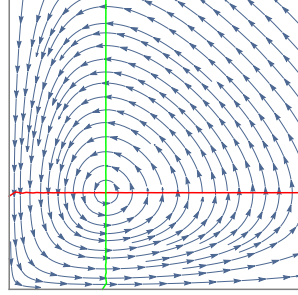
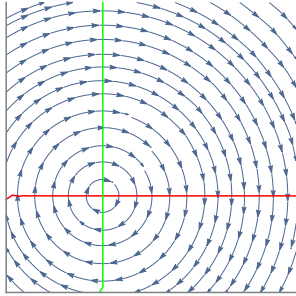
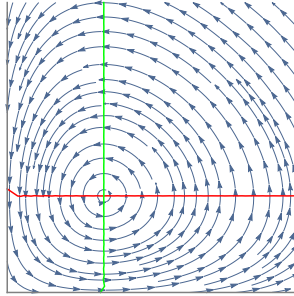


Figure 2 Case $(a_1, b_3) = (0, 0)$, $a_3 \leq -1$, and $b_1 \leq -1$. All solutions starting in \mathbb{R}_+^2 are periodic.

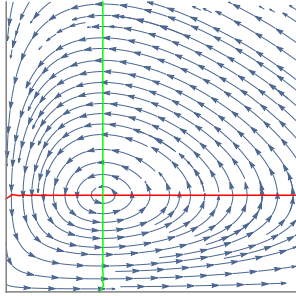
$$\begin{aligned} a_1 &= 0 = b_3, \\ a_3 &> 0, b_1 > 0 \end{aligned}$$



$$\begin{aligned} a_1 &= 0 = b_3, \\ -1 &< a_3 < 0, -1 < b_1 < 0 \end{aligned}$$



$$\begin{aligned} a_1 &= 0 = b_3, \\ -1 &< a_3 < 0, b_1 \leq -1 \end{aligned}$$



$$\begin{aligned} a_1 &= 0 = b_3, \\ a_3 &\leq -1, -1 < b_1 < 0 \end{aligned}$$

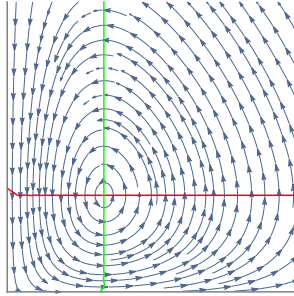


Figure 3 Case $(a_1, b_3) = (0, 0)$, $a_3 b_1 > 0$, and at least one of $a_3 \leq -1$ and $b_1 \leq -1$ is violated. Top left: $a_3 > 0$ and $b_1 > 0$ (both the x -axis and the y -axis are approached by some orbits). Top right: $-1 < a_3 < 0$ and $-1 < b_1 < 0$ (both the x -axis and the y -axis are approached by some orbits). Bottom left: $-1 < a_3 < 0$ and $b_1 \leq -1$ (the y -axis is approached by some orbits). Bottom right: $a_3 \leq -1$ and $-1 < b_1 < 0$ (the x -axis is approached by some orbits).

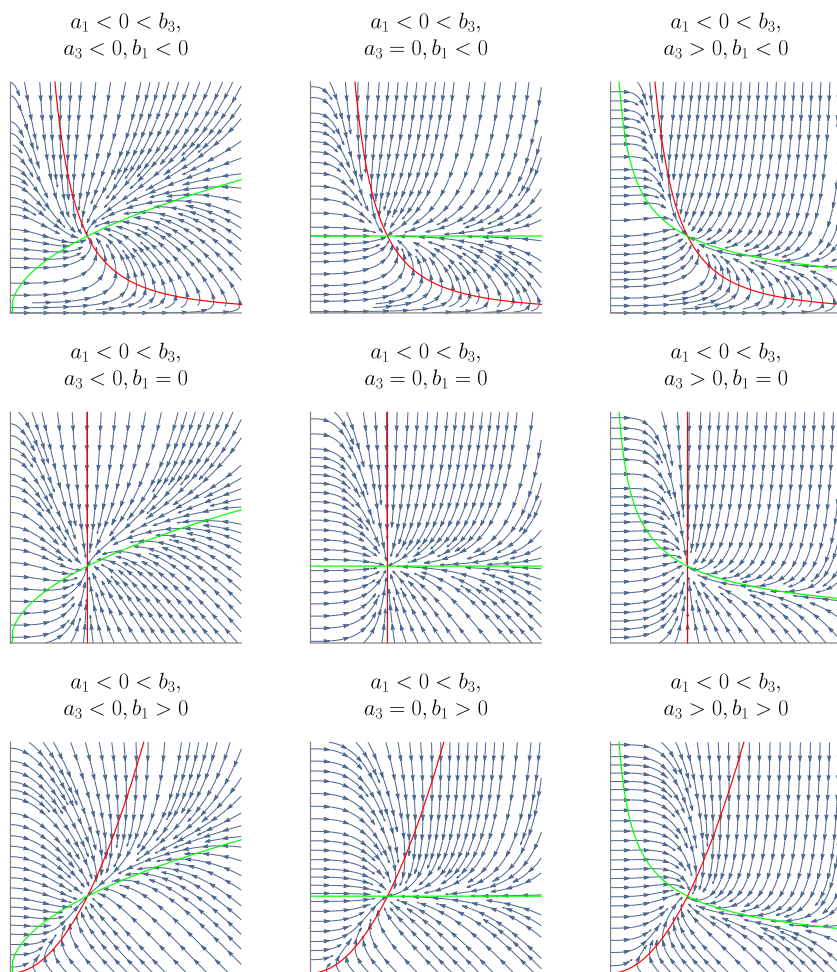


Figure 4 Case $a_1 < 0 < b_3$ and $\det C < 0$. No solution approaches the boundary of the positive quadrant, and there is no unbounded solution.

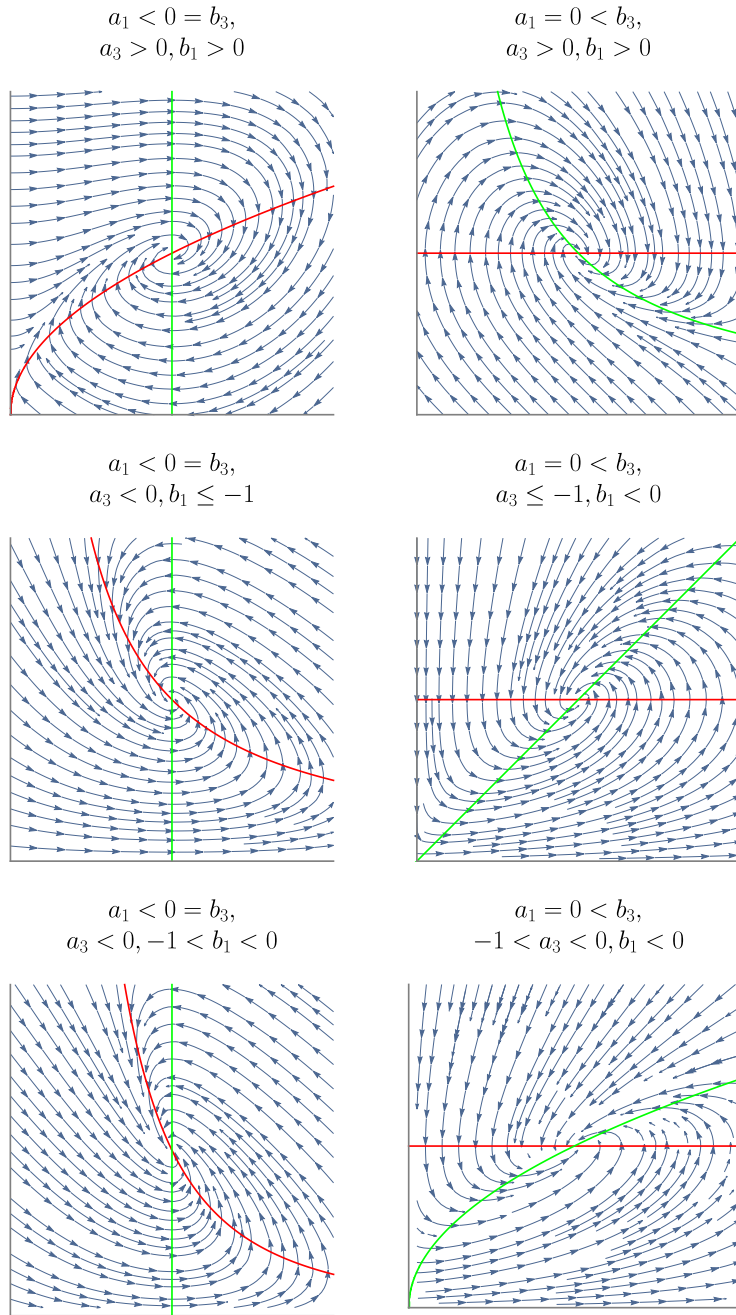


Figure 5 Cases $a_1 < 0 = b_3$ and $a_1 = 0 < b_3$ (and $\det C < 0$). In the top and bottom row, some solutions approach the boundary of the positive quadrant, while in the middle row no solution approaches the boundary.

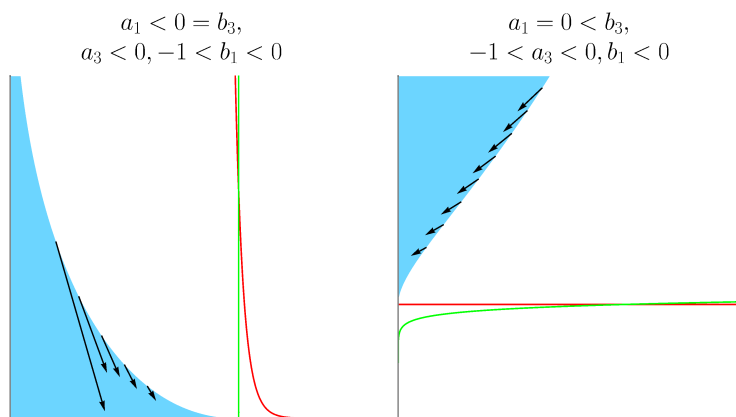


Figure 6 The forward invariant sets constructed in Subsection 4.3.3.

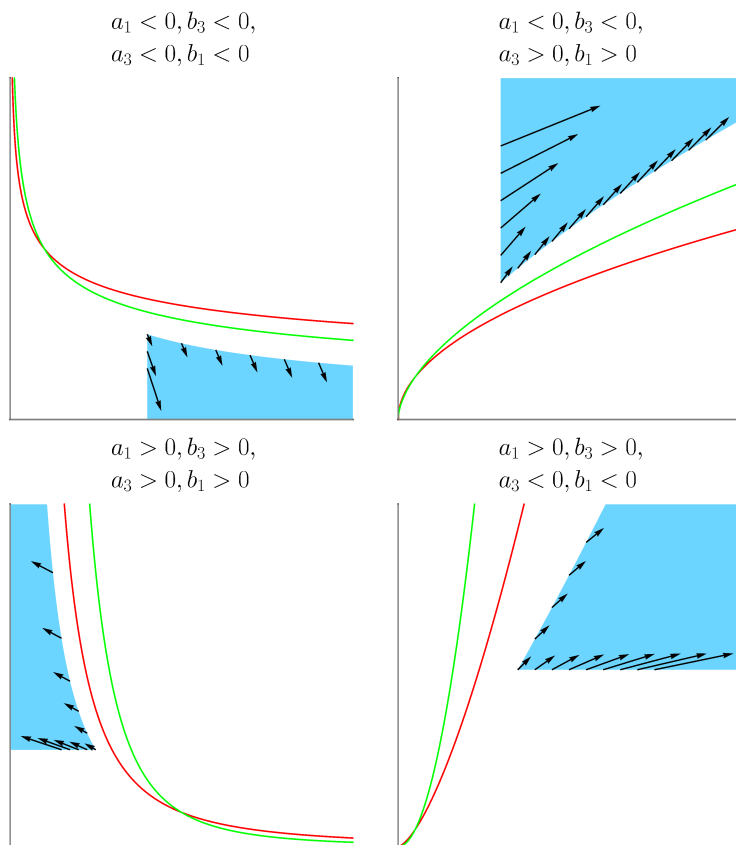


Figure 7 The forward invariant sets constructed in Lemmas 11 (top left), 12 (top right), 13 (bottom left), and 14 (bottom right).

$$1 < \alpha \leq \frac{3}{2},$$

$$\alpha - 1 \leq \beta \leq 2 - \alpha$$

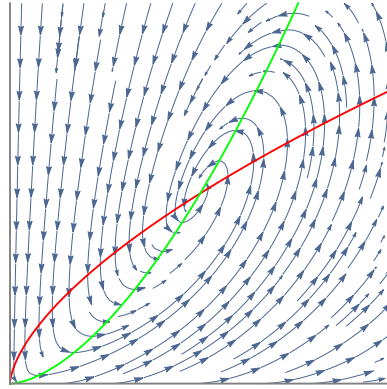
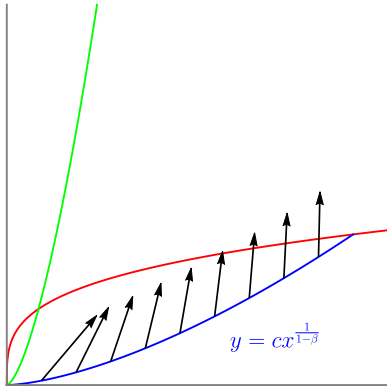


Figure 8 Case $1 < \alpha \leq \frac{3}{2}$ and $\alpha - 1 \leq \beta \leq 2 - \alpha$ for the ODE (15). Global asymptotic stability is proved in Subsection 4.5.2.

$$1 < \alpha \leq \frac{3}{2},$$

$$\alpha - 1 \leq \beta \leq 2 - \alpha$$



$$1 < \alpha \leq \frac{3}{2},$$

$$\alpha - 1 \leq \beta \leq 2 - \alpha$$

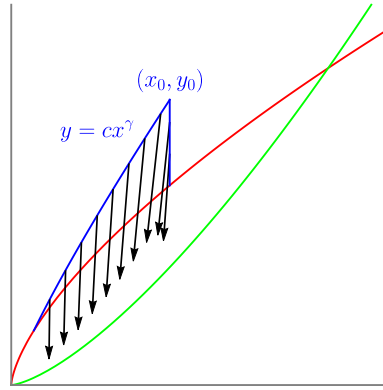


Figure 9 Lemma 16: every solution starting below the x -nullcline with $x > 1$ eventually reaches the x -nullcline (left). Lemma 17: every solution starting above the x -nullcline with $y > 0$ small enough eventually reaches the x -nullcline (right).